Chapter 8
Response of *Marginopora vertebralis* (*Foraminifera*) from Laucala Bay, Fiji, to Changing Ocean pH

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Introduction

Climate change and human activities have increased the release and accumulation of greenhouse gases, such as CO_2, into the atmosphere (Gattuso and Lavigne 2009). Emissions of CO_2 into the atmosphere over the past two centuries, combined with changes in land use and terrestrial vegetation, have resulted in increasing concentration of dissolved CO_2 in the ocean. The resulting impact on marine carbonate chemistry has been called a phenomenon called ocean acidification (e.g., Feely et al. 2004; Caldeira and Wickett 2005; Cao and Caldeira 2008; Gattuso and Hansson 2011). As CO_2 dissolves in seawater (H_2O), it combines with water molecules to form HCO_3^- and H^+ ions, the latter increasing the acidity of seawater and decreasing pH. The world oceans have already taken up about 50% of the anthropogenic CO_2 released (Sabine 2004). The recent global mean pH is 8.1, which is 0.1 pH units below the pre-industrial value of the open surface ocean (Sabine 2004). The International Panel on Climate Change (IPCC) predicted future scenarios, indicating that the atmospheric CO_2 will increase to concentrations as much as 970 ppm by the year 2100 (IPCC 2013). The continuous increase in CO_2 concentrations likely will result in a pH decrease of 0.46 units by 2100 (Caldeira

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and Wickett 2005). Reduced carbonate ion concentrations and saturation state will require greater energy expenditure for organisms to calcify (Erez 2003). An increasing number of field and laboratory studies are indicating negative impacts on marine calcifying organisms, such as corals and foraminifera (Kleypas et al. 1999; Riebesell et al. 2000; Doo et al. 2014 and references therein).

The most abundant shelled organisms, and second-most abundant carbonate-precipitating organisms (after coccolithophorids), in the world's oceans are the Foraminifera. Their shells are commonly known as "tests". The most abundant foraminifers in the upper oceans precipitate calcium carbonate for their test formation by seawater vacuolization (Erez 2003). According to Erez (2003), the calcification is manifested by the formation of organic matrix where the granules provide Ca^{2+} for the first calcium carbonate crystals. These crystals precipitate over previously formed chambers, providing the overall shape of the foram. The bulk of the calcification process continues with secondary lamination involving vacuolization of seawater and is responsible for bulk of skeletal deposition. The secondary calcification occurs in a delimited space created by the pseudopodia (Erez 2003).

Based on the absence of calcareous benthic foraminifera in acidic seawater associated with natural seafloor venting of carbon dioxide in a variety of shallow-water locations, Uthicke et al. (2013) concluded that, if ocean acidification continues at predicted rates, many benthic foraminifera will be extinct by 2100. However, Pettit et al. (2013) did not find a significant response in the benthic foraminiferal assemblages to reduced pCO_2 in deeper shelf and slope settings.

Similarly, laboratory experiments examining responses of calcareous foraminifera to lower pH and elevated pCO_2 have shown significant differences among different taxa and even within the same species (Doo et al. 2014). The majority of studies have shown that pH lower than 7.8 can have deleterious effects on calcareous benthic foraminifera (Kuroyanagi et al. 2009; Dias et al. 2010; Fujita et al. 2011; Vogel and Uthicke 2012; McIntyre–Wressnig et al. 2013; Knorr et al. 2015). These effects include reduced calcification (Kuroyanagi et al. 2009; Moy et al. 2009; Haynert et al. 2011) and decreased growth rates (Manno et al. 2012; Reymond et al. 2012), indicating the decline in carbonate sediment production by foraminifera as ocean acidification proceeds (Dias et al. 2010; Knorr et al. 2015). However, a few studies have reported increased rates of calcification at responded to increased pCO_2 (e.g., Fujita et al. 2011; Vogel and Uthicke 2012).

The present study investigated the effects of ocean acidification on the growth of *Marginopora vertebralis* Quoy and Gaimard (1830). Larger benthic foraminifers, such as *M. vertebralis,* produce calcite skeletons and are major contributors to sand production on reef flats that nourish the beaches in Pacific Islands. Our working hypothesis was that *M. vertebralis* are sensitive to changes in seawater carbonate chemistry such that reduced pH should affect their ability to form calcareous tests. *Marginopora vertebralis* lives in the shallowest reef-associated environments (i.e., the intertidal and shallow subtidal zone) and is an important producer of sediment in Fijian beaches (Sharma 2007); its demise could have serious consequences for beach stability, especially under rising sea level.

Methods

Sample Collection

The samples of *M. vertebralis* were collected from Makuluva and Nukubuco reefs on the Suva Barrier Reef (Fig. 8.1). Sharma (2007) identified a total of 68 different species of benthic foraminifers in the Nukubuco Reef flat in Laucala Bay, including abundant *M. vertebralis*. Moreover, Sharma cultured living specimens to study growth, abundance and reproduction of marine benthic foraminifers.

The location of the collection site was determined using GPS data. Salinity and temperature of the sample collection area were assessed using an YSI-85 m. The map of Viti Levu is enlarged in Fig. 8.1c to show the research site. During low tide

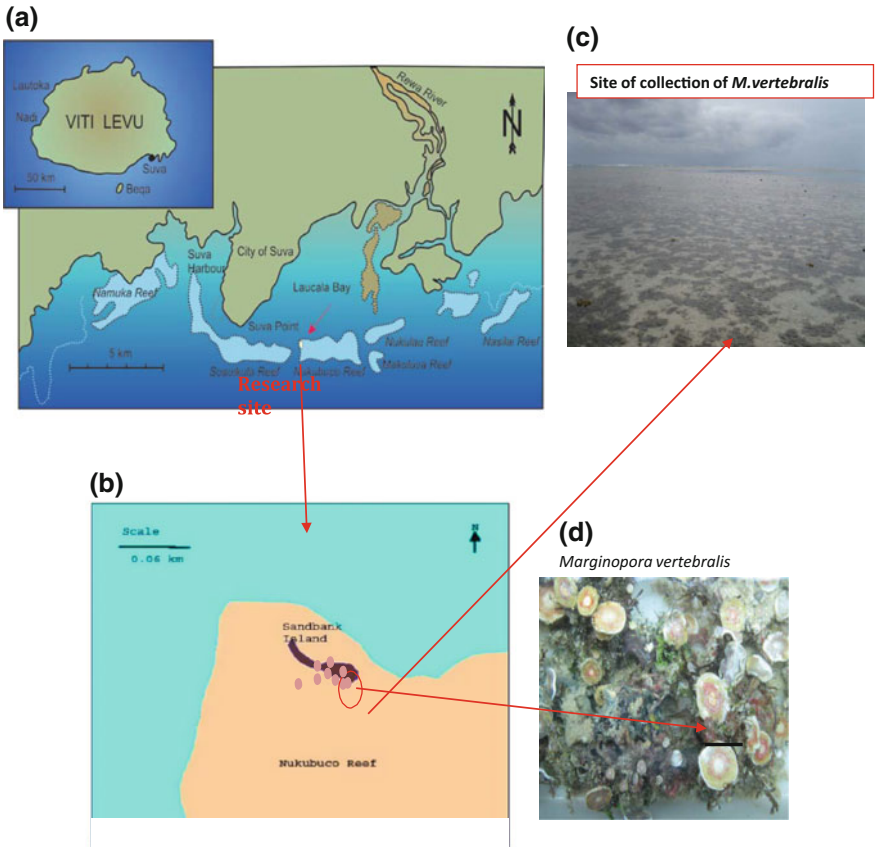

Fig. 8.1 **a** Map of Laucala Bay; **b** the mapping of the site of collection of *Marginopora vertebralis;* **c** algal flat habitat between Sandbank Island and Nukubuco Reef; and **d** *M. vertebralis* attached to algae and coral (*arrow*). *Scale bars* **a** 5 km; **b** 0.06 km (*Source*: SOPAC 2012; Sharma 2007); **d** 1 cm

(0.3 m), *M. vertebralis was* easily collected as it is large enough to be identified in situ. The foraminifers and associated sediments were collected using hand scoops and immediately placed in an aerated aquarium with filtered seawater, where they were kept overnight. The next day, *M. vertebralis* specimens had crawled upward and attached themselves to the sides of the aquarium and therefore could be easily identified and removed, based on the methods of Sharma (2007).

Natural seawater (salinity 33.0), contained in 35 L reservoir tanks, was acidified by means of a bubbling system supplying CO_2 gas (Fig. 8.2). The gas, saturated with water vapour (to limit evaporation) was injected through the water as very fine bubbles allowing the gas to rapidly dissolve. The seawater pH in the reservoirs was monitored using a flat-surface, combination pH electrode (YSI Environmental pH 100). Once the pH reached the required level, the supply of CO_2 was halted via an automated feedback relay system (Accu-Max pH controller). As the acidified water was pumped from the reservoir to supply the experimental tanks, the overflow water was returned to the reservoir. Whenever the pH increased, CO_2 bubbling was triggered to ensure that the desired pH level was maintained. Each reservoir contained a CO_2 Reactor, an air pump and a water pump. The reservoirs were refilled with natural seawater (pH 8.1) every 10 days from a separate 300 m^3 seawater tank, causing the pH in the reservoir tank to increase. This increase triggered the supply of CO_2 to be restarted and CO_2 continued to bubble through the water until the pH was reduced to the required level. Using this method it was possible to supply large quantities of CO_2 acidified seawater with a consistent pH. Two seawater acidification reservoir tanks (pH 7.8, pH 7.5) and one control (ambient pH 8.1) were maintained. From each tank, water was supplied to the corresponding three small tanks (25 × 10 × 15 cm) where the *M. vertebralis* specimens were cultured.

The experimental setup diagram (Fig. 8.2) shows how the connections were made from the reservoirs to the connecting tanks and vice versa. The CO_2 system is plugged with pH controllers (adjusted at pH 7.8 and 7.5). The CO_2 is released with the help of the bubble counter, check valve and CO_2 injector. The pH controller regulates and stabilizes the pH in the reservoirs and the peristaltic pump helps in the circulation of seawater, creating an ocean-like environment. Nine (4.5 L) tanks (3 treatments with 3 replicates each) were placed in a room (ambient temperature ~27.5 ºC) and connected to a pH controller system (Fig. 8.2). Each tank was individually supplied with seawater at a rate of approximately 3.3 $mlmin^{-1}$ using a peristaltic pump. The *M. vertebralis* specimens were randomly assigned to one of the three pH treatment levels (8.1 [ambient seawater], 7.8, and 7.5).

The treatments were maintained under a 12-h light and 12-h dark cycle using a T5 Aquarium lamp with a light intensity of 42.5 $wattsm^{-2}$. Acidification of the seawater did not begin until 24 h after the *M. vertebralis* specimens were placed in their treatment tanks. Seawater pH was reduced gradually over a period of two days and the experiment started when the final water chemistry for each treatment was reached. The experiment ran for 11 weeks, during which time, the pH of the water supplied to the tanks was monitored daily via a pH controller (Accu Max I). Samples for Total Alkalinity were taken at the beginning of the experiment and then once per week throughout the duration of the experiment. The values given by the

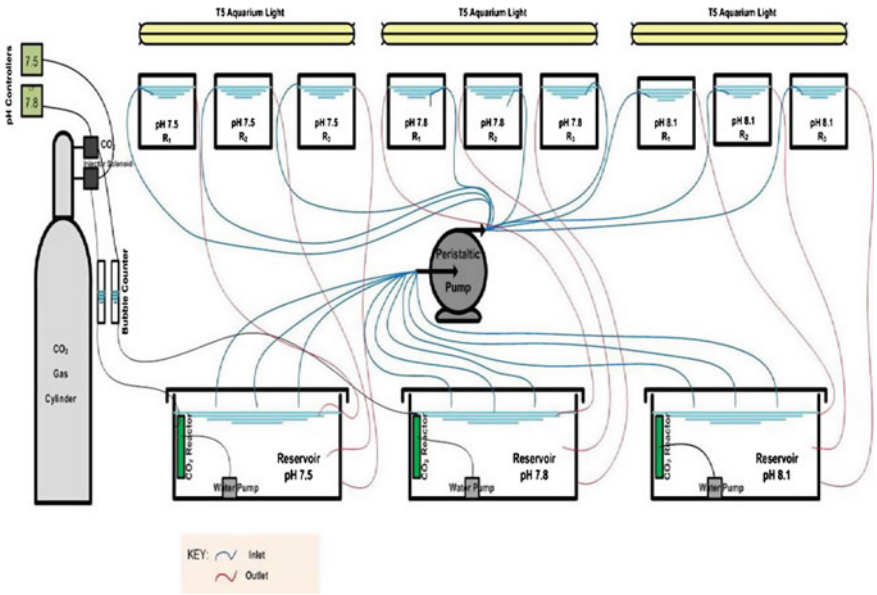

Fig. 8.2 Experimental set-up model

pH electrodes in the reservoir tanks were cross-checked every week against values measured by a regularly calibrated pH meter (InLab 413SG, Mettler–Teledo).

The carbonate chemistry in the culture media was determined using the following procedures and calculations (Pawlowski 1994). Borosilicate bottles, used to collect the water samples for alkalinity measurements, were rinsed with concentrated HCl, followed by at least five rinses with deionised water. Seawater samples were collected from the experimental aquaria. Borosilicate bottles were fully filled and tightly capped. Analysis was carried out within 6 h of sample collection. To standardize acid used in titrations, 10 ml aliquot of 0.01 M sodium tetraborate was placed into a 250 ml conical flask and a few drops of mixed indicator were added. The aliquot was titrated with 0.01 M HCl until the end point was reached (color changed from green to purple). The titre was recorded for the calculation of HCl concentration:

$$\text{Conc of HCl} = \frac{\text{Vol. of Borax} \times \text{Mass of Borax} \times 1000 \times 2}{\text{Vol. of titre} \times 381.37 \times 100}$$

To determine the total alkalinity (A_T) of a sample, 50 ml of the water sample were pipetted into a 250 ml Erlenmeyer flask and few drops of phenolphthalein indicator were added. Once the solution color turned pink, it was titrated with 0.01 M HCl until the color disappeared and the volume of added acid was recorded. Then 2–3 drops of mixed bromocrescol green/methyl red indicator were added to

the same solution and titrated with standardized 0.01 M HCl to a pink color. Then A_T was calculated using this formula:

$$\text{Total Alkalinity, } A_T(\text{mg/L}) = \frac{A \times M \times 50,000}{\text{Sample volume}}$$

where A = Volume of standard HCl used (ml)

$$M = \text{Molarity of HCl}$$

The MATLAB program CO2SYS (single-input mode directly adapted from Lewis et al. 1998) was used to calculate and present seawater parameters where the salinity was constant at 35 and temperature was constant at 27.5 °C. The input temperature and pressure were from measurements performed in the laboratory. There are four measurable parameters of the aquatic carbon dioxide system: pH, pCO_2, total dissolved inorganic carbon (DIC) and total alkalinity (TA). The measured pH and alkalinity values were entered into the program. The equilibrium constants from Mehrbach et al. (1973) as refit by Lueker et al. (2000) on a total scale were used. The measurements made by Mehrbach et al. (1973) were made on real seawater.

Input variables (input conditions):

- Salinity (35), Temperature (27.5 °C) and Pressure (1 atm).
- Total Si (optional) and Total Phosphate (optional). If left empty, the total Si and total P concentrations are assumed to be zero in the calculations.
- Two (2) known CO_2 parameters (TA, pH).

Output (for both "input" and "output" conditions):

- The other CO_2 parameters (pCO_2), total dissolved inorganic carbon [DIC].
- Contributions to the alkalinity.
- Carbonate speciation.

Growth Assessments

The maximum diameter (d) of the specimens at the start of the experiments ranged from $0.4 \leq d \leq 1.4$ cm. The 25 *M. vertebralis* specimens in each treatment were weighed prior to the start of the experiment and once each week as a group using an analytical balance (Libror-Aex 200 g). The specimens were collected using hand scoops, pat dried using tissue, and wet weights of the group of specimens from each replicate of each treatment were determined.

To assess linear growth, Calcein (-bis [N, N-bis (carboxymethyl) aminomethyl]-fluorescein) was used to fluorescently label existing chambers in *M. vertebralis*. Calcein makes newly formed chambers distinguishable when the specimens are

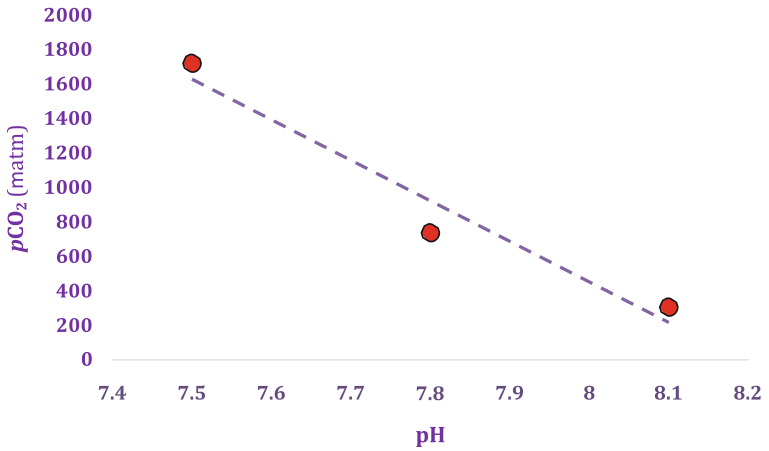

Fig. 8.3 pCO_2 in seawater of two pH treatments (7.5 and 7.8) and control (8.1)

viewed under a confocal microscope (Dissard et al. 2009). Prior to placement of the specimens into their treatment tanks, the foraminifers were placed in a solution at 40 µM of Calcein for approximately 48 h to allow the incorporation of the green fluorescent cell marker (Fig. 8.3). Once Calcein is incorporated inside the cells, Calcein AM (a nonfluorescent molecule) is hydrolyzed by endogeous esterase into the highly negatively charged green-fluorescent Calcein. The fluorescent Calcein is retained in the cytoplasm in living cells but is not incorporated into the subsequently added chambers (Papadopoulos et al. 1994). At the end of the experiment, this technique helps to distinguish between the pre-existing (stained) and the newly grown (unstained) calcite (Bernhard et al. 2004; Dissard et al. 2009).

Growth of the selected specimens was assessed using confocal imagery (Nikon ECLIPSE TE2000-U). The portion of the radius of the calcite shell added after Calcein incubation revealed growth that occurred during experimental treatments. The ruler property from EZC_1 3.91 imaging software was used to determine the increase in radius in µm. The mean increases in radius at each treatment for each replicate was recorded.

Results

Seawater Chemistry

Seawater chemistry contrasted strongly between the 2 treatments and control, with mean values ranging from 8.1 to 7.5 pH units and 309 to 1717 matm pCO_2, respectively. Mean total alkalinity was 2277 µmol kg^{-1} (n = 11, SD = 101). The alkalinity values were between 2176 and 2408 µmol kg^{-1}, a range we used together with the pH measurements from all aquaria (treatments) to calculate pCO_2 concentrations (Table 8.1).

Table 8.1 Carbonate system parameters in the experiment. Temperature (T), salinity (S), total alkalinity (A_T), and the total scale pH (pH_T) were measured directly. The treatment and control values are mean of measurements (n = 11) taken weekly over the course of the experiment. The remaining values were calculated based on methods of Lewis et al. (1998), with equilibrium constants from Mehrbach et al. (1973) as refit by Lueker et al. (2000) on total scale. Partial pressure of CO_2 in seawater (pCO_2) is in milliatmospheres (matm); [OH^-] is given in mmolkg^{-1}, A_T, [HCO_3^-] and [CO_3^{2-}] is given in mmolkg^{-1} SW

pH treatment	T ° C	S	pH_T	A_T mmolkg^{-1} SW	pCO_2 matm	[OH^-] mmolkg^{-1}	[HCO_3^-] mmolkg-^{1} SW	[CO_3^{2-}] mmolkg^{-1} SW
8.1	27.5	35	8.1 (0.05)	2176	309.1	9.66	1577.3	240.6
7.8	27.5	35	7.8 (0.05)	2247	738.5	4.84	1891.4	144.6
7.5	27.5	35	7.5 (0.05)	2408	1717	4.8	2203.5	84.5

The pH measurements correlated with the long term averages of pCO_2 for the two treatments and control (Fig. 8.3, $R^2 = 0.95$).

Growth in M. vertebralis

We cultured 225 *M. vertebralis* individuals in all, 25 specimens per replicate, and three replicates at three different pH values: pH 7.5, 7.8, and 8.1 (control). Specimens cultured at pH 7.5 showed a 429 μm mean increase in radius, while in those at pH 7.8, the mean increase in radius was 441 μm (Table 8.2). At pH 8.1, the mean increase in radius was 1024 μm, which was more than double the increase noted for pH 7.5 and 7.8. Similarly, the masses of the 25 *M. vertebralis* specimens from each replicate of each treatment (Table 8.2) also revealed limited growth at pH 7.5 averaging 10.2 ± 3.6 mg per specimen, with slightly more at pH 7.8, averaging 14.5 ± 3.7 mg. The specimens cultured at pH 8.1 grew an average of 30.0 ± 5.7 mg. The relationship between increase in radius and increase in mass are shown in Fig. 8.4. The relative weight gain (%) by the 25 individuals of *M. vertebralis* at each pH treatment during 11 week experiment revealed that the specimens in the pH 7.5 treatments grew on average by 3.24%, whereas individuals at pH 7.8 grew on average by 4.24%. At pH 8.1, average growth was 8.39% for the 11 weeks culture. The shell growth in *M. vertebralis* was negatively related to elevated pCO_2 (Fig. 8.5) and was positively related to increased CO_3^{2-} (Fig. 8.6).

Other Observations

At the end of the experiment, most specimens contained pale pink cytoplasm, which indicated that they were alive throughout the entire experimental period. Several specimens reproduced asexually. When an individual about to reproduce, its color changes to white with a pale purple ring in the middle. During reproduction

Table 2 The mean increase in individual test radius and test weight, both assessed after 11 weeks

Treatment	Replicate	Increase in radius (μm)	Increase in weight (mg)
7.5	R_1	471 ± 102	6.05
	R_2	489 ± 77	12.3
	R_3	326 ± 23	12.3
	Mean ± SD	429 ± 89	10.2 ± 3.6
7.8	R_1	476 ± 43	8.71
	R_2	480 ± 31	13.1
	R_3	367 ± 38	11.7
	Mean ± SD	441 ± 64.1	14.5 ± 3.7
8.1	R_1	1019 ± 346	24.3
	R_2	785 ± 107	27.3
	R_3	1267 ± 306	35.4
	Mean ± SD	1024 ± 241	30.0 ± 5.7

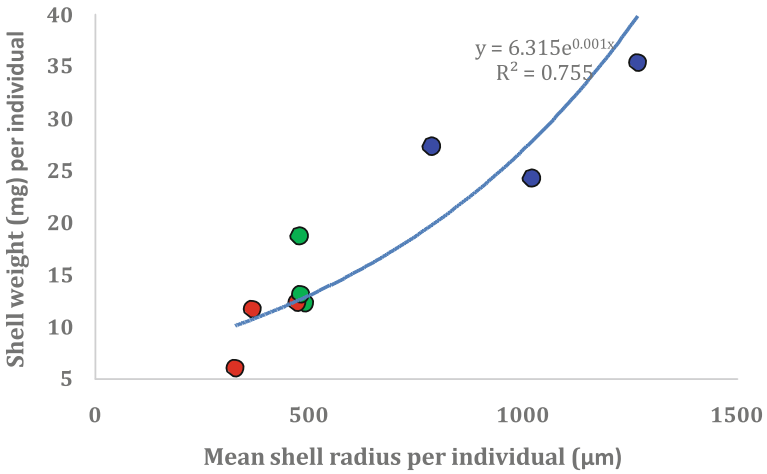

Fig. 8.4 Relationship between increase in shell radius and in average shell weight of *Marginopora vertebralis* measured after 11 weeks in culture (*red*—pH 7.5, *green*—pH 7.8, and *blue*—pH 8.1) (Color figure online)

(Fig. 8.7), the parent shell becomes white as the endoplasm containing the dinoflagellate symbionts is incorporated into the megalospheric offspring. Reproduction was only noted at the pH treatment of 8.1.

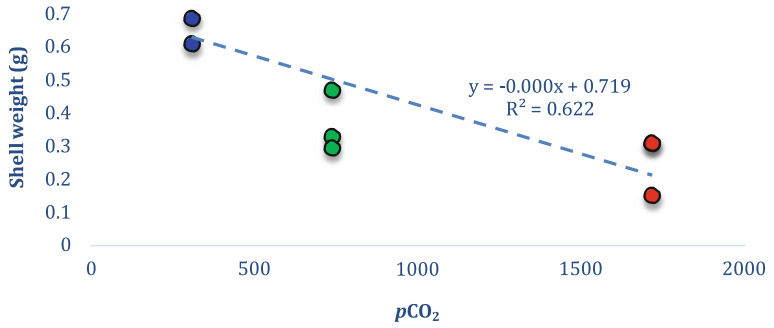

Fig. 8.5 Mean increase in shell weight of 25 *M. vertebralis*, grouped by pH level (n = 11) at three pCO_2 levels

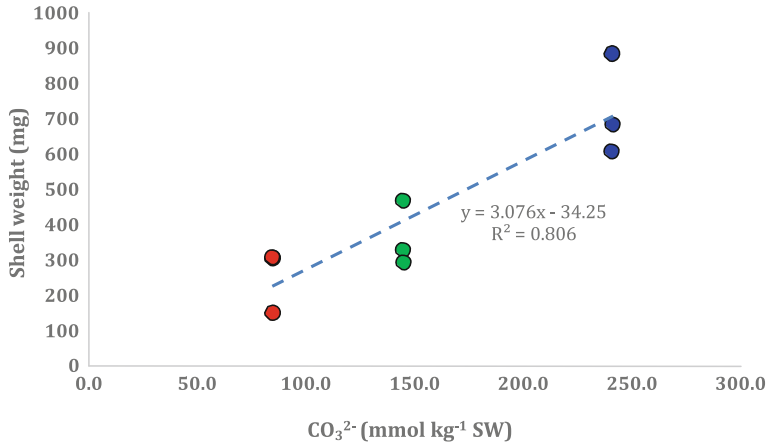

Fig. 8.6 Mean shell weight (mg) of 25 *M. vertebralis*, grouped by treatment (n = 11) against CO_3^{2-} (mmol kg^{-1} SW)

Discussion

Our experimental results revealed that growth in *Marginopora vertebralis* can be inhibited at pH of 7.5 and 7.8 compared to growth in ambient seawater at pH 8.1. This inhibition occurred with respect to growth in diameter of the experimental specimens and in addition of mass to the shells (i.e., calcification). Our results are consistent with the majority of previous studies that have shown that pH lower than 7.8 can have deleterious effects on calcareous larger benthic foraminifers (Kuroyanagi et al. 2009; Dias et al. 2010; Fujita et al. 2011; Vogel and Uthicke 2012; McIntyre–Wressnig et al. 2013; Knorr et al. 2015). These effects have included reduced calcification (Kuroyanagi et al. 2009; Moy et al. 2009; Haynert et al. 2011) and decreased growth rates (Manno et al. 2012; Reymond et al. 2012).

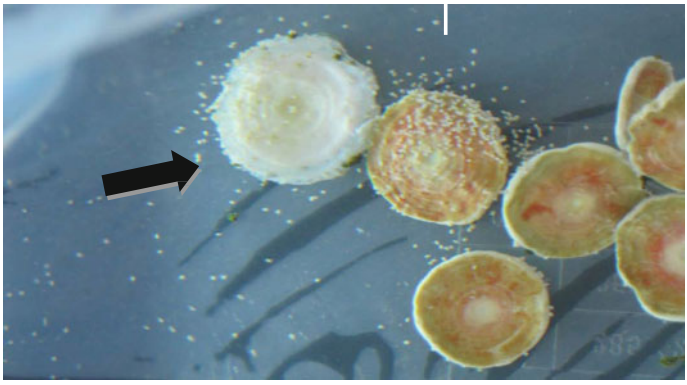

Fig. 8.7 Reproduction of *Marginopora vertebralis* at pH treatment 8.1 (*black arrow*)

However, as Doo et al. (2014) demonstrated in their review of studies examining responses of calcareous foraminifers to lower pH and elevated pCO_2, differences in responses among different taxa and even within the same species have been reported. For example, Vogel and Uthicke (2012) reported that *M. vertebralis* responded to increased pCO_2 with increased rates of calcification from laboratory experiments, while Uthicke and Fabricius (2012) reported reduced calcification in both field studies and laboratory observations.

More recent studies have added to the uncertainties and questions, as Sinutok et al. (2014) reported reduced growth under elevated pCO_2, Schmidt et al. (2014) reported somewhat mixed results, and Prazeres et al. (2015) found no influence of elevated pCO_2 on calcification. However, Schmidt et al. (2014) were largely examining response to elevated temperature, as their lowest pH was 7.9. Prazeres et al., on the other hand, were working at a relatively low temperature of 24 °C. Thus, the most logical conclusion that can be drawn from what may seem to be contradictory results are that a variety of environmental factors are influencing growth and calcification, even in well controlled experiments. The ambient seawater used in different experiments in different laboratories likely differs in salinity, nutrients, dissolved organic matter or trace element. Food available to the experimental specimens certainly differs among experiments, as do ambient light conditions.

What also remains to be determined is whether *M. vertebralis* exposed to elevated pCO_2 for an entire life cycle can acclimate or if long-term exposure will result in decreased calcification rates, as has been observed for other benthic foraminifera (Dissard et al. 2010; Fujita et al. 2011; Haynert et al. 2011; Knorr et al. 2015). Moreover, the combined effects of temperature, nutrient availability and CO_3^{2-} need to be studied to estimate the impact of oceanic environmental changes on *M. vertebralis* calcite production. The studies by Schmidt et al. (2014) and Prazeres et al. (2015) provide models in examining the interactions of pH and other parameters, and also in examining other physiological responses of the foraminifers.

Conclusions

The shells of larger foraminifers on the reef flats of coral islands in the Indo-Pacific can make up as much as 90% of the sand-sized sediments (e.g., Hallock 1981; Fujita et al. 2016). While uncertainties remain regarding the range of environmental factors that influence calcification in *M. vertebralis*, our observations that growth and calcification in *M. vertebralis* decreases as a function of decreasing [CO_3^{2-}] in seawater indicate that increasing pCO_2 in this century could reduce carbonate production by important larger foraminifers such as *M. vertebralis* at least by half. While this estimate is conservative compared to those of Uthicke et al. (2013), who predicted extinction of many taxa, or Knorr et al. (2015), who estimated an 85% reduction in carbonate production by some major taxa, loss of even 50% of the carbonate sand production by larger benthic foraminifers could be devastating for low lying coral islands surrounded by reef flats. Reductions in the major source of sand- sized sediments at the same time that sea level is rising clearly compounds the threats associated with climate change for human residents of low-lying islands.

Future Research Topics

- Future studies may seek to culture other important species of foraminifera around Fiji and compare their response to increasing ocean acidity.
- Modeling and documentation of carbonate production differences in Foraminifera in a historical context, along with present and future projections will be vital to determine coastal protection and conservation strategies.

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